Rheology of Active Filament Solutions

T. B. Liverpool[1,3] and M. C. Marchetti[2]
[1]*Department of Applied Mathematics, University of Leeds, Woodhouse Lane, Leeds LS2 9JT, UK*
[2]*Physics Department, Syracuse University, Syracuse, NY 13244, USA and*
[3]*Kavli Institute for Theoretical Physics, UCSB, Santa Barbara, CA 93106, USA*
(Dated: February 4, 2008)

We study the viscoelasticity of an active solution of polar biofilaments and motor proteins. Using a molecular model, we derive the constitutive equations for the stress tensor in the isotropic phase and in phases with liquid crystalline order. The stress relaxation in the various phases is discussed. Contractile activity is responsible for a spectacular difference in the viscoelastic properties on opposite sides of the order-disorder transition.

Soft active systems are exciting examples of a new type of condensed matter where stored energy is continuously transformed into mechanical work at microscopic length scales. A realization of this are polar filaments interacting with associated molecular motors in the cell cytoskeleton[1,2]. These systems are characterized by a variety of dynamic and stationary states which the cell accesses as part of its cycle[3,4,5]. Recent experimental and theoretical studies of the dynamics of solutions of active filaments have focused on the formation of both homogeneous and inhomogeneous states with spatial structures, such as bundles, vortices or asters [4,5,6,7,8,9,10,11,12,13,14].

In this letter we study the effect of motor activity on the rheological properties of active solutions under an externally imposed stress. Understanding the viscoelasticity of cells, and cellular extracts in-vitro, is a very important problem currently receiving a lot of experimental attention[15,16,17,18,19]. From a theoretical point of view describing the mechanics of the cytoskeleton in its full complexity remains very challenging. As a first step in this direction we focus here on using methods from polymer physics to understand the effect of motor activity on the viscoelasticity of a dilute solution of long stiff biopolymers. A phenomenological description of the rheology of isotropic suspensions of active particles near the isotropic-nematic transition was proposed recently by Hatwalne et al.[20]. The present work provides a microscopic basis for their results and a general framework for analyzing the viscoelastic behavior of active solutions in both isotropic and ordered states.

Our model makes several testable predictions. First we find that, as suggested in Ref.[20], activity yields a contribution to the viscosity of an isotropic solution that diverges at the isotropic-nematic transition (see Fig. 1). Such a diverging viscosity is reminiscent of an equilibrium liquid-solid transition rather than a liquid-liquid transition, and is a direct consequence of the active-stresses. Unlike a liquid-solid transition, however, the divergence is localized at the IN transition and the viscosity is finite in the nematic phase. A second novel signature of activity in the stress relaxation is found in the nematic phase, where the shear stress acquires a nonequilibrium contribution proportional to ATP (Adenosine Tri-Phosphate) consumption rate that remains finite for zero deformation rate. In other words, an active nematic solution is driven into a state with a non-vanishing macroscopic stress by the energy input from ATP hydrolysis, even in the absence of an externally applied mechanical deformation. This non-equilibrium contribution is also present in the normal stresses in the nematic phase.

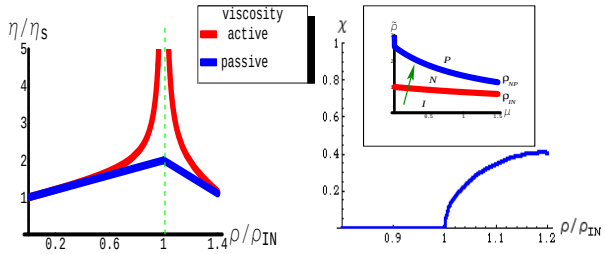

FIG. 1: (a) The steady-state shear viscosity on both sides of the IN transition for passive and active nematics.(b) The 'motility' parameter, χ (see Eq. (20)) relating the magnitude of the active component of shear stress to the 'activity' μ ($\sim$ ATP consumption) Inset: phase diagram showing the IN transition.

We consider a suspension of polar filaments in a thin film of height comparable to the length of the filaments (quasi-two dimensions) and a constant density m of motor clusters. A concentration $\rho(\mathbf{r},t)$ of filaments is suspended in an incompressible solvent of viscosity η_0 characterized by a fluid velocity $\mathbf{v}(\mathbf{r},t)$, with $\boldsymbol{\nabla}\cdot\mathbf{v}=0$. Momentum conservation yields

$$\rho_s\left(\partial_t\mathbf{v}+\mathbf{v}\cdot\boldsymbol{\nabla}\mathbf{v}\right) \;=\; \boldsymbol{\nabla}\cdot\boldsymbol{\sigma}^s+\boldsymbol{\nabla}\cdot\boldsymbol{\sigma}^f\;, \qquad (1)$$

with ρ_s the (constant) density of the solution. The solvent contribution to the stress tensor is

$$\boldsymbol{\nabla}\cdot\boldsymbol{\sigma}^s=\eta_0\nabla^2\mathbf{v}-\nabla p\;,$$

with p the pressure. The filament contribution, $\boldsymbol{\sigma}^f$, must be determined in terms of the driving forces (velocity gradients, $\kappa_{ij}=\partial_j v_i$, and motor activity, μ $\sim$ ATP consumption rate) and the conserved and order parameter fields describing the filaments,

$$\boldsymbol{\sigma}^f=\boldsymbol{\sigma}^f(\rho,\mathbf{p},S_{ij};\boldsymbol{\kappa},\mu)\;, \qquad (2)$$

where $\mathbf{p}$ and S_{ij} are the local polarization and nematic alignment tensor that describe the orientational order of

the filaments. The derivation of this constitutive equation from a model of filament dynamics is one of the central outcomes of work.

The filaments are modeled as hard rods of *fixed* length l and diameter a ($l \gg a$) at position $\mathbf{r}$ with filament polarity characterized by a unit vector $\hat{\mathbf{u}}$. The filament contribution to the stress tensor is[21]

$$\boldsymbol{\nabla}\cdot\boldsymbol{\sigma}^f \;=\; -\int_{\mathbf{r}_1}\int_{\hat{u}_1} c(\mathbf{r}_1,\hat{\mathbf{u}}_1,t)\Big\langle\delta\left(\mathbf{r}-\mathbf{r}_1-s\hat{\mathbf{u}}\right)\mathcal{F}(s)\Big\rangle_s \;,$$

where $\mathcal{F}(s)$ is the hydrodynamic force per unit length on a rod at position s along the rod, $\langle..\rangle_s \equiv \int_{-l/2}^{l/2} ds...$, and $c(\mathbf{r},\hat{\mathbf{u}},t)$ is the concentration of polar filaments with position/orientation $\{\mathbf{r},\hat{\mathbf{u}}\}$. The force on the rod is specified by its interaction with the solvent, other rods, and the motor clusters. For low Reynolds numbers $\mathrm{Re}\ll 1$, viscous effects dominate inertia and we can set the left hand side of Eq. (1) to zero.

We calculate the force per unit length $\mathcal{F}(s)$ by decomposing a rod into a sequence of beads of diameter a and solving self-consistently for the flow field around the rod[21] on scales much bigger than a. The stress due to the filaments is (to $\mathcal{O}(\nabla^2)$)

$$\begin{aligned}\nabla\cdot\boldsymbol{\sigma}^f(\mathbf{r},t) \;&=\; \int_{\hat{\mathbf{u}}}\mathbf{f}(\mathbf{r},\hat{\mathbf{u}},t)\\ &\quad-\int_{\hat{\mathbf{u}}}\Big\langle\big(\frac{s}{l}\big)^2\left(\frac{\hat{\mathbf{u}}\cdot\nabla}{l}\right)\boldsymbol{\tau}(\mathbf{r},\hat{\mathbf{u}},t)\Big\rangle_s \;, \quad (3)\end{aligned}$$

where

$$\begin{aligned}\mathbf{f}(\mathbf{r},\hat{\mathbf{u}},t) \;&=\; c\left[k_BT_a\boldsymbol{\nabla}\ln c+\boldsymbol{\nabla}U_x-\mathbf{F}_a(\mathbf{r},\hat{\mathbf{u}},t)\right] \;,\\ \boldsymbol{\tau}(\mathbf{r},\hat{\mathbf{u}},t) \;&=\; c\left[k_BT_a\mathcal{R}\ln c+\mathcal{R}U_x-\mathbf{T}_a\right]\times\hat{\mathbf{u}}\\ &\quad -c\frac{\zeta_\perp}{2}\hat{\mathbf{u}}\hat{\mathbf{u}}(\hat{\mathbf{u}}\cdot\nabla)\cdot\mathbf{v}(\mathbf{r}) \;, \quad (4)\end{aligned}$$

with $U_x(\mathbf{r},\hat{\mathbf{u}}) = k_BT\int_{\hat{\mathbf{u}}'}\int_{\boldsymbol{\xi}} c(\mathbf{r}+\boldsymbol{\xi},\hat{\mathbf{u}}')$ the excluded volume potential. The force density has contributions from fluctuations or diffusion (both thermal and non-thermal - hence the *active temperature* $T_a \neq T$), excluded volume, and motor activity. There is also a viscous contribution to the stress proportional to the velocity gradient ($\zeta_\perp = 4\pi\eta_0 l/\ln(l/a)$).

The active force and torque are given by

$$\begin{aligned}\mathbf{F}_a(\mathbf{r},\hat{\mathbf{u}}_1) &= -m_0\int_{\hat{\mathbf{u}}_2}\big\langle\boldsymbol{\zeta}(\hat{\mathbf{u}}_1)\cdot\mathbf{v}_a(1;2)c(\mathbf{r}+\boldsymbol{\xi},\hat{\mathbf{u}}_2)\big\rangle_{s_1,s_2} \;,\\ \mathbf{T}_a(\mathbf{r},\hat{\mathbf{u}}_1) &= -m_0\int_{\hat{\mathbf{u}}_2}\big\langle\zeta_r\boldsymbol{\omega}_a(1;2)c(\mathbf{r}+\boldsymbol{\xi},\hat{\mathbf{u}}_2)\big\rangle_{s_1,s_2} \;, \quad (5)\end{aligned}$$

where $m_0 = ma^2$, $(1;2)\equiv(s_1,\hat{\mathbf{u}}_1;s_2,\hat{\mathbf{u}}_2)$, $\boldsymbol{\xi} = \hat{\mathbf{u}}_1 s_1 - \hat{\mathbf{u}}_2 s_2$ and $\boldsymbol{\zeta}(\hat{\mathbf{u}}) = \zeta_\perp(\boldsymbol{\delta}-\hat{\mathbf{u}}\hat{\mathbf{u}}) + \zeta_\parallel\hat{\mathbf{u}}\hat{\mathbf{u}}$, with $\zeta_\perp$, $\zeta_\parallel$ and ζ_r friction coefficients. The angular velocity is taken as $\boldsymbol{\omega}_a = 2\left[\gamma_0+(\hat{\mathbf{u}}_1\cdot\hat{\mathbf{u}}_2)\,\gamma_1\right](\hat{\mathbf{u}}_1\times\hat{\mathbf{u}}_2)$, with γ_0 and γ_1 motor-induced rotation rates proportional to ATP consumption, and tends to align filaments.[24] The motor-induced translational velocity has been derived from a model of motors walking along the filaments at a mean rate β. It has the form $\mathbf{v}_a(1;2) = \frac{1}{2}\mathbf{v}_r + \mathbf{V}_m$, with[24]

$$\begin{aligned}\mathbf{v}_r \;&=\; \frac{\tilde{\beta}}{2}(\hat{\mathbf{u}}_2-\hat{\mathbf{u}}_1)+\frac{\tilde{\alpha}}{2l}\boldsymbol{\xi} \;,\\ \mathbf{V}_m \;&=\; A\,(\hat{\mathbf{u}}_2+\hat{\mathbf{u}}_1)+B\,(\hat{\mathbf{u}}_2-\hat{\mathbf{u}}_1) \;,\end{aligned}$$

where $\tilde{\alpha} = \alpha(1+\hat{\mathbf{u}}_1\cdot\hat{\mathbf{u}}_2)$ and $\tilde{\beta} = \beta(1+\hat{\mathbf{u}}_1\cdot\hat{\mathbf{u}}_2)$. The parameter $\alpha \sim \beta(a/l)$ is controlled by spatial inhomogeneities in the motor stepping rate. Momentum conservation yields expressions for A and B. For long thin rods with $\zeta_\perp = 2\zeta_\parallel \equiv 2\zeta$, to leading order in $\hat{\mathbf{u}}_1\cdot\hat{\mathbf{u}}_2$, we find $A = -[\beta-\alpha(s_1+s_2)/2]/12$ and $B = \alpha(s_1-s_2)/24$. When evaluating the contribution to the stress tensor, only terms up to first order in $\hat{\mathbf{u}}_1\cdot\hat{\mathbf{u}}_2$ are retained in the active force $\boldsymbol{\zeta}(\hat{\mathbf{u}}_1)\cdot\mathbf{v}_a(1;2)$ exerted by a motor cluster on the filament in the first of Eqs. (5). This approximation only affects the numerical values of the coefficients in the stress tensor, not its general form.

The concentration $c(\mathbf{r},\hat{\mathbf{u}},t)$ of polar filaments satisfies a local conservation law,

$$\partial_t c + \boldsymbol{\nabla}\cdot(\mathbf{v}c) + \mathcal{R}\cdot(\boldsymbol{\omega}c) + \boldsymbol{\nabla}\cdot\mathbf{J} + \mathcal{R}\cdot\mathcal{J} = 0 \;, \quad (6)$$

where $\boldsymbol{\omega} = \hat{\mathbf{u}}\times\boldsymbol{\kappa}\cdot\hat{\mathbf{u}}$ and $\mathcal{R} = \hat{\mathbf{u}}\times\frac{\partial}{\partial\hat{\mathbf{u}}}$. The translational and rotational currents in Eq. (6) contain diffusive, excluded volume and active contributions,[24] $\mathbf{J} = -\boldsymbol{\zeta}^{-1}(\hat{\mathbf{u}})\cdot\mathbf{f}(\mathbf{r},\hat{\mathbf{u}})$, $\mathcal{J} = -\zeta_r^{-1}\boldsymbol{\tau}(\mathbf{r},\hat{\mathbf{u}})$, with $\mathbf{f}$ and $\boldsymbol{\tau}$ given by Eqs. (4).

The conserved and broken symmetry fields are the density $\rho(\mathbf{r},t)$, polarization $\mathbf{p}(\mathbf{r},t)$, and nematic order $S_{ij}(\mathbf{r},t)$, defined as moments of the probability distribution, $\int_{\hat{\mathbf{u}}} c(\mathbf{r},\hat{\mathbf{u}},t) = \rho(\mathbf{r},t)$, $\int_{\hat{\mathbf{u}}}\hat{\mathbf{u}}\,c(\mathbf{r},\hat{\mathbf{u}},t) = \rho(\mathbf{r},t)\mathbf{p}(\mathbf{r},t)$, $\int_{\hat{\mathbf{u}}}\hat{Q}_{ij}\,c(\mathbf{r},\hat{\mathbf{u}},t) = \rho(\mathbf{r},t)S_{ij}(\mathbf{r},t)$, where $\hat{Q}_{ij} = \hat{u}_i\hat{u}_j - \frac{1}{2}\delta_{ij}$. Continuum equations for these fields are obtained from Eq. (6) by the coarse-graining procedure described in Ref.[24].

The constitutive equation for the stress tensor $\boldsymbol{\sigma}^f$ is obtained by evaluating the right hand side of Eq. (3). For simplicity we consider spatially homogeneous solutions in the presence of a constant velocity gradient κ_{ij}. To lowest order in gradients, the three contributions to the stress tensor of the filaments are

$$\sigma^f_{ij}(\mathbf{r},t) = \sigma^P_{ij}(\mathbf{r},t) + \sigma^A_{ij}(\mathbf{r},t) + \sigma^v_{ij}(\mathbf{r},t) \;, \quad (7)$$

with passive and active contributions, $\boldsymbol{\sigma}^P$ and $\boldsymbol{\sigma}^A$, given by

$$\begin{aligned}\sigma^P_{ij} \;&=\; 2k_BT_a\rho\Big[\Big(1-\frac{\rho}{\rho_{IN}}\Big)S_{ij}-\frac{\rho}{2\rho_{IP}}\big(p_ip_j-\frac{1}{2}p^2\delta_{ij}\big)\\ &\quad+\frac{1}{2}\delta_{ij}\Big(1+\frac{l^2\rho}{\pi}\big(1-\frac{2}{3}S^2\big)\Big)\Big] \;, \quad (8)\\ \sigma^A_{ij} \;&=\; \mu k_BT_a\rho^2\Big[\frac{8}{9}\big(S_{ij}+\frac{1}{2}\delta_{ij}\big)+\frac{2}{3}\big(p_ip_j+\frac{1}{2}p^2\delta_{ij}\big)\\ &\quad+\frac{1}{9}(1-S^2)\delta_{ij}\Big] \;, \quad (9)\end{aligned}$$

where $\mu = \frac{m_0\alpha l^3}{48D}$, $\rho_{IP} = D_r/(m_0\gamma_0 l^2)$, and $\rho_{IN} = \rho_N/[1+\rho_N l^2 m_0\gamma_1/(4D_r)]$ is the density for the isotropic-nematic (IN) transition at finite motor density[24], with $\rho_N = 3\pi/(2l^2)$ the density of the IN transition in passive systems. Finally, the viscous contribution to the stress is

$$\sigma^v_{ij} = \frac{l\rho\zeta_\perp}{24}\Big[\frac{1}{2}\big(\kappa^s_{ij}+\tfrac{1}{2}\kappa_{kk}\delta_{ij}\big)+\frac{1}{3}\big(\delta_{ij}\kappa_{kq}S_{qk}+S_{ij}\kappa_{kk}\big) +\kappa^s_{ik}S_{kj}+\kappa^s_{jk}S_{ki}\Big] , \quad (10)$$

with $\kappa^s_{ij} = (\kappa_{ij}+\kappa_{ji})/2$.

In agreement with Ref.[20], we find that active units generate force dipoles in the fluid yielding contributions to the stress which are equilibrium-like, i.e., have the same form as those appearing in an equilibrium solution, but with new contractile stresses ($\alpha > 0$) which have no analogue in their equilibrium counterparts.

For a homogeneous solution ρ = constant and the equations for polarization and nematic order parameter are obtained by averaging Eq. (6) over $\hat{\mathbf{u}}$,

$$\partial_t p_i = -\Omega_i - D_r\Big(1-\frac{\rho}{\rho_{IP}}\Big)p_i +2D_r\Big(\frac{2\rho}{\rho_{IN}}-\frac{\rho}{\rho_{IP}}\Big)S_{ij}p_j , \quad (11)$$

$$\partial_t S_{ij} = -\Omega_{ij} - 4D_r\Big(1-\frac{\rho}{\rho_{IN}}\Big)S_{ij} +\frac{2D_r\rho}{\rho_{IP}}\Big(p_ip_j-\frac{1}{2}\delta_{ij}p^2\Big) . \quad (12)$$

with $\rho\Omega_i = \int d\hat{\mathbf{u}}\hat{u}_i\boldsymbol{\mathcal{R}}\cdot(\boldsymbol{\omega}f)$ and $\rho\Omega_{ij} = \int d\hat{\mathbf{u}}\hat{Q}_{ij}\boldsymbol{\mathcal{R}}\cdot(\boldsymbol{\omega}f)$. We find

$$\Omega_i = -\kappa_{ij}p_j+\frac{1}{2}\Big[\kappa^s_{ij}p_j+\tfrac{1}{2}\kappa_{kk}p_i\Big] , \quad (13)$$

$$\Omega_{ij} = -\frac{1}{2}\big[\kappa^s_{ij}-\tfrac{1}{2}\delta_{ij}\kappa_{kk}\big]-\big(\kappa_{ik}S_{kj}+\kappa_{jk}S_{ki}\big) +\frac{1}{3}\Big[S_{ij}\kappa_{kk}+\delta_{ij}S_{kl}\kappa_{kl}+2(S_{ik}\kappa^s_{kj}+S_{jk}\kappa^s_{ki})\Big] . \quad (14)$$

The homogeneous (bulk) steady-states are obtained by setting the rhs of the order parameter equations to zero. We find (I)sotropic ($\mathbf{p}=0, S_{ij}=0$), (N)ematic ($\mathbf{p}=0, S_{ij}\neq 0$) and (P)olarized ($\mathbf{p}\neq 0, S_{ij}\neq 0$) phases. It can be shown using Eqs. (8,9) that in a *stationary* bulk fluid the passive contribution to the stress tensor is identically zero in each phase, while the active contribution is non-zero. In the following we consider the geometry of pure shear flow with $\kappa_{ij} = \dot{\epsilon}\delta_{ix}\delta_{jy}$ and discuss the *linear* viscoelastic response of the active solution in the isotropic (I), polarized (P) and nematic (N) phases.

a. Isotropic phase In the isotropic phase close to the IN transition a shear flow builds up nematic order, yielding a non-zero value for S_{ij} to $\mathcal{O}(\dot{\epsilon})$. The shear stress is linear in the strain rate, $\sigma_{xy} = \mathcal{O}(\dot{\epsilon})$, while the normal stress is quadratic, $\sigma_{xx}-\sigma_{yy} = \mathcal{O}\left(\dot{\epsilon}^2\right)$. To linear order we obtain $\big(\partial_t + 1/\tau_A\big)S_{xy} = \dot{\epsilon}/4$, with

$$\frac{1}{\tau_A} = \frac{4}{\tau_0}\Big(1-\frac{\rho}{\rho_{IN}}\Big) , \quad (15)$$

where $\tau_0 = 1/D_r$ and $D_r = k_BT_a/\zeta_r$ the rotational diffusion constant. The time scale τ_A diverges as we approach the *active* IN transition. In a sheared sample, the total stress (filaments + solution) is

$$\sigma_{xy} = \tilde{\eta}\dot{\epsilon}+2k_BT\left(1-\frac{\rho}{\rho_{IN}}\right)\rho S_{xy}+\frac{8}{9}\mu k_BT\rho^2 S_{xy} , \quad (16)$$

where $\tilde{\eta} = \eta_0(1+\frac{\pi l^2\rho}{24})$. The first contribution is from the solvent and the viscous stress, the second is from the passive stress, and the third from active stresses.

For an oscillatory applied shear we define the frequency dependent shear viscosity $\sigma_{xy}(\omega) = \eta_A(\omega)\dot{\epsilon}$, with low frequency limit

$$\eta_A = \tilde{\eta}+\frac{k_BT\rho}{8D_r}\Big(1+\frac{16}{9}\tau_A D_r\mu\Big) . \quad (17)$$

This *diverges* as we approach the $I-N$ transition (see Fig. 1). This behavior should be contrasted to that of a passive solution of rods near the *equilibrium* I-N transition. In this case the stress relaxation time $\tau_P = D_r^{-1}/(1-\rho/\rho_N)$ also diverges at the IN transition, but the zero-frequency viscosity, $\eta = \tilde{\eta}+k_BT\rho/(8D_r)$, remains *finite*, as required by the Fluctuation-Dissipation Theorem.

b. Nematic phase In the nematic phase, there is the possibility of alignment of the nematic director by the shear flow. The director $\mathbf{n}$ and the magnitude S of the nematic order parameter are defined by $S_{ij} = S\left(\hat{n}_i\hat{n}_j-\delta_{ij}/2\right)$. The equation of motion for the director in a steady shear flow is obtained from Eq. (12),

$$\partial_t\hat{n}_i = \left(\delta_{ij}-\hat{n}_i\hat{n}_j\right)\hat{n}_k\frac{\Omega_{jk}}{S} . \quad (18)$$

Defining $\hat{\mathbf{n}} = (\cos\theta, \sin\theta)$, we obtain a steady state solution for the director orientation given by $\cos 2\theta = 2S$. For $S > 1/2$ there are no steady-state solutions, possibly pointing to the existence of periodic or chaotic solutions characterized by "wagging" or "kayaking" of the nematic director[25].

The steady-state expression for the stress tensor in the *active* nematic state is obtained from Eqs. (8) and (9) as

$$\sigma_{ij} = -\frac{k_BT\rho}{2D_r}\left(\frac{\Omega_{ij}}{\rho}\right)+\sigma^A_{ij}+\sigma^v_{ij} , \quad (19)$$

from which the 6 Leslie coefficients of the active nematic can be obtained using Eqs. (9),(10) and (14)[21,26].

The novel nature of the constitutive equation is best illustrated by the simple case of an active nematic in the *flow-aligning* regime ($S < 1/2$), where the steady-state shear stress is given by

$$\sigma_{xy} = \eta\dot{\epsilon}+\chi\mu , \quad (20)$$

where $\eta = \tilde{\eta}+\frac{k_BT}{2D_r}\rho\left(\frac{1}{4}-S^2\right)\left(1+D_r\tau'_A\frac{16\tilde{\alpha}\rho}{9}\right)$ and $\chi = \frac{8}{9}k_BT\rho^2S\sqrt{\frac{1}{4}-S^2}$, with $1/\tau'_A = 8D_r\left(\rho/\rho_{IN}-1\right)$. The

magnitude of nematic order S relaxes on a time scale τ'_A while the director relaxes on the shear time scale $\dot{\epsilon}$ leading to non-monotonic stress relaxation.

The signature of this constitutive equation is a shear stress that does not vanish for zero deformation rate. This is because the active filament system is being driven out of equilibrium by two sources of energy. One external, due to the shear, and the other internal, due to the activity of the motors (see Fig. 1). The viscosity diverges as the IN transition is approached from the nematic side, but it decreases dramatically as one goes deeper into the nematic phase (see Fig. 1). This is a direct consequence of flow alignment as S increases with density. All corrections to η vanish at $S = 1/2$, where the flow-aligned regime ceases to exist.

Another signature of a nematic phase is that the normal stresses are of first order in the shear rate. In addition, in an active nematic one obtains an anomalous constitutive equation,

$$\sigma_{yy} - \sigma_{xx} = \eta_N \dot{\epsilon} + \chi_N \mu \ , \tag{21}$$

where $\eta_N = \frac{k_B T}{2D_r} \rho S \sqrt{\frac{1}{4} - S^2}$ and $\chi_N = \frac{8}{9} k_B T \rho^2 2 S^2$.

Both the anomalous stresses (shear and normal) should be easily observed by performing linear rheological experiments on active filaments in the nematic phase at varying shear rates.

c. Polarized phase In a polarized state, with $\mathbf{p} = p_0 \hat{\mathbf{p}}$, a uniform density and a constant velocity gradient, the unit vector $\hat{\mathbf{p}}$ satisfies the dynamical equation

$$\partial_t \hat{p}_i + \omega_{ij} \hat{p}_j = \lambda \delta^T_{ij} \kappa^s_{jk} \hat{p}_k \ , \tag{22}$$

where $\lambda = 1/2$, $\omega_{ij} = (\kappa_{ji} - \kappa_{ij})/2$ and $\delta^T_{ij} = (\delta_{ij} - \hat{p}_i \hat{p}_j)$. Voituriez et al. [14] have recently suggested that spontaneous flow can be obtained in active polar materials, corresponding to a state with finite velocity gradients and flow alignment. Flow alignment, however, can only occur for $\lambda > 1$, while the present (low density) calculation yields $\lambda = 1/2$. Corrections to λ can be obtained by incorporating the fact that fact that the alignment tensor is slaved to the polarization field. However an analysis of such corrections shows that they fail to increase λ to values larger than 1, suggesting that no steady uniformly flowing polarized state exists for a thin film in the low density limit presented here. An interesting alternative is the possibility of periodic or chaotic states[27].

In summary, we have used a molecular model to study the macroscopic mechanical response of active filament solutions in both isotropic and ordered states. Motor activity leads to a novel coupling of mechanical properties to order and to anomalous constitutive equations in the liquid crystalline state. The theoretical framework developed here can be generalized to consider stress inhomogeneities. This is relevant for understanding the microrheology of active filament systems where new behavior is expected even in the isotropic regime[26].

Acknowledgments TBL acknowledges the support of the Royal Society and the National Science Foundation under Grant No. PHY99-07949. MCM acknowledges support from the National Science Foundation, grants DMR-0305407 and DMR-0219292.

[1] B. Alberts et al., *Molecular Biology of the Cell* (Garland, New York, 2002).
[2] J. Howard, *Mechanics of Motor Proteins and the Cytoskeleton* (Sinauer, New York, 2000).
[3] K. Takiguchi, J. Biochem. **109**, 520 (1991); R. Urrutia et al., PNAS **88**, 6701 (1991).
[4] F. J. Nédélec et al, Nature **389**, 305 (1997).
[5] T. Surrey et al, Science **292**, 1167 (2001).
[6] H. Nakazawa and K. Sekimoto, J. Phys. Soc. Jpn. **65**, 2404 (1996).
[7] K. Kruse and F Jülicher, Phys. Rev. Lett. **85**, 1778 (2000); Phys. Rev. E, **67**, 051913 (2003).
[8] T. B. Liverpool and M. C. Marchetti, Phys. Rev. Lett. **90**, 138102 (2003); ibid **93**, 159802 (2004). F Ziebert and W. Zimmermann, Phys. Rev. Lett. **93**, 159801 (2004).
[9] H. Y. Lee and M. Kardar, Phys. Rev. E **64**, 56113 (2001).
[10] R. A. Simha and S. Ramaswamy, Phys. Rev. Lett. **89**, 058101 (2002).
[11] K. Kruse et al, Phys. Rev. Lett. **92**, 078101 (2004); Eur. Phys. J. E **16**, 5 (2006).
[12] S. Sankararaman et al., Phys. Rev. E **70**, 031905 (2004)
[13] I. S. Aranson and L. S. Tsimring, Phys. Rev. E **71**, 050901(R) (2005).
[14] R. Voituriez, J. F. Joanny, and J. Prost, Phys. Rev. Lett. **96**, 28102 (2006).
[15] M. Tempel, G. Isenberg and E.Sackmann, Phys. Rev. E. **54**, 1802-1810 (1996).
[16] D. Humphrey et al, Nature (London) **416**, 412 (2002).
[17] J. H. Shin, M. L. Gardel, L. Mahadevan, P. Matsudaira, and D. A. Weitz, PNAS **101**, 9636 (2004).
[18] M. M. A. E. Claessens, R. Tharmann, K. Kroy, and A. R. Bausch, Nature Phys. **2**, 186 (2006).
[19] G. Danuser and C. M. Waterman-Storer, Ann. Rev. Biophys. Biomol. Struct. **35**, 361 (2006).
[20] Y. Hatwalne, S. Ramaswamy, M. Rao, and R. A. Simha, Phys. Rev. Lett. **92**, 118101 (2004).
[21] M. Doi and S. F. Edwards, *The theory of polymer dynamics* (Oxford University Press, New York, 1986).
[22] A model of the cluster as a torsional spring of constant κ gives $\gamma_0 \sim \gamma_1 \sim D_r \kappa / k_B T$.
[23] T.B. Liverpool and M. C. Marchetti, Europhys. Lett. **69**, 846 (2005).
[24] A. Ahmadi, M.C. Marchetti, T.B. Liverpool, Phys. Rev. E. **72**, 060901(R) (2005); submitted to Phys. Rev. E (2006).
[25] Y-G Tao, W. K. den Otter, and W. J. Briels, Phys. Rev. Lett. , **95**, 237802 (2005) .
[26] T.B. Liverpool and M.C. Marchetti, unpublished (2006).
[27] B. Chakrabarti et al, Phys. Rev. Lett. **92** , 055501 (2004).